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Who let the dogs in? A review of the recent genetic evidence for the introduction of the dingo to Australia and implications for the movement of people

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ABSTRACT

The phylogenetic origin of the dingo (*Canis dingo*) is an enigma. Introduced to Australia during the Holocene, debate continues regarding the exact timing of its introduction and whether it was by early agriculturalists, hunter-gatherers or sea-faring traders. The expanding array of genetic research on both dog domestication and dingoes adds fuel to this debate. Here we synthesise recent genetic studies of dingo origins. We then evaluate a list of potential groups who could have been responsible for their introduction, and suggest that Toalean or other hunter-gatherers from south Sulawesi were the likely suspects. We conclude with suggestions for further archaeological and genetic research that have the potential to clarify not just the origin of the dingo, but the movement of people around Oceania (here broadly defined as the entire insular region between South East Asia and Australia), and by extrapolation, aspects of Holocene cultural change.

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1. Introduction

The relationship between dogs and humans is one of the most defining symbiotic relationships in the history of humanity. Dogs were the first species to be domesticated by people, with some arguing this relationship began as long as 35,000 years ago (Ovodov et al., 2011). Dogs witnessed human dispersal around the world, stood beside people for the rise of cereal domestication (even evolving genetically to digest grains) (Axelsson et al., 2013), played a role in the evolution of human hunting, and some speculate in the extinction of Neanderthals (Shipman, 2015; Taçon and Pardoe, 2002). In short, dogs have been an integral part of the development of complex social organization, and generally, where there were modern humans, there were dogs ... well, mostly. The spread of dogs to Australia is an exception - archaeological evidence suggesting the dingo (*Canis dingo*, Crowther et al., 2014), did not reach the continent until the mid-late Holocene (3500–5000 kya) (Fillios et al., 2012). If dogs and humans walked together for potentially 30,000 years, why did it take so long for people to bring canines south? In Australia, dogs appear to be a relatively late arrival – post-dating human settlement by at least some 40,000 years. How did dogs get to Australia, when, why and by whom?

This paper addresses just one of these many questions, and asks who brought the first dog (dingo) to Australia? Here we review the recent genetic evidence for the dingo's origins (Table 1, Fig. 1) and propose

there were at least five different groups of people who could have introduced dogs: Indian mariners, Lapita peoples, a Timor group, Taiwanese peoples and Toalean hunter gatherer peoples from south Sulawesi. Drawing on the genetic evidence for the dingo's origins, augmented by the archaeological record, we evaluate the evidence for each group, and suggest the most parsimonious answer may well be an immediate origin in Sulawesi.

Given the symbiotic nature of the canine-human relationship, understanding the origin of the dingo will enable us to better understand the movement of people around Oceania (Australia, South East Asia). Importantly, understanding potential contact with people outside of Australia will contribute to understanding the raft of significant human behavioural and cultural changes that characterize the Holocene (10,000 BP–present) in this part of the world (cf. Lourandos, 1983). Dogs are not only important as the first human domesticate, but also as the only one whose domestication predates the emergence of agriculture, making them a valuable proxy for human hunter-gatherer migrations (Larson and Bradley, 2014; Larson et al., 2012; Zeder et al., 2006).

2. Background

2.1. Holocene Australia

Unravelling the origins of the dingo has the potential to contribute valuable information about the movement of peoples around Oceania during a period of significant cultural change. Frequently encompassed by the term 'intensification' (Lourandos, 1983), Holocene changes

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include demographic shifts as reflected in a higher frequency of archaeological sites and artefact densities (e.g. [Attenbrow, 1987](#); [Hughes and Lambert, 1982](#); [Johnson and Brook, 2011](#); [Lourandos, 1983](#); [Morwood, 1987](#); [McConnell and O'Connor, 1999](#); [Ross, 1985](#); [Smith and Ross, 2008](#)), changes in human technology, characterized by an increase in backed artefacts, points, tulas, adzes ([Gould, 1969](#); [Hiscock and Attenbrow, 1998](#)), increased rock art diversity and regionalisation (e.g. see [Flood, 1997](#); [Layton, 1992](#); [Taçon, 1993, 2011](#)) and a shift in the exploitation of prey species to smaller body sizes ([Dortch, 2004a, 2004b](#); [Dortch and Wright, 2010](#); [Fillios et al., 2010](#); [Morwood, 1987](#)). The driving forces behind these cultural and technological changes are still debated, with changing subsistence strategies aimed at risk reduction ([Hiscock, 1994](#)), climate change ([Dortch, 2004a, 2004b](#); [Dortch and Wright, 2010](#); [Johnson and Wroe, 2003](#)) and the interaction between human intensification and increased ENSO variability ([Prowse et al., 2013](#)) all cited as factors. The dingo may also be one of these driving factors of change, and thus potentially an important element in constructing Holocene dynamics. The arrival of a new commensal species would almost certainly have made an impact on aspects of human subsistence strategies – perhaps altering hunting practices or changing the types of species exploited (e.g. [Balme and O'Connor, in this issue](#); [Fillios et al., 2010](#)). Either of these possibilities could have had a flow on effect that might be seen in technological changes (e.g. shift in artefact type).

Diffusionist explanations for cultural change have lost popularity since the 1960s, with [Hiscock \(1994, 2008\)](#) and [Hiscock and Attenbrow \(1998\)](#) arguing in several places for an adaptive model to explain these changes. A more recent wave of human migration (or simply contact) is rarely viewed as a serious potential factor in Holocene cultural transformations. It is commonly accepted that from arrival in Australia to first European contact, Aboriginal Australians were genetically isolated. Uncovering the spatio-temporal origins of the dingo could potentially change this assertion. While recent genetic research corroborates archaeological data suggesting that Australia has the earliest evidence for the expansion of anatomically modern humans out of Africa (65,000 + years, see [Rasmussen et al., 2011](#); [Reich et al., 2011](#)), the genetic history of Aboriginal Australians is just beginning to be explored in better detail ([Nagle et al., 2016](#)) to address the possibility of subsequent contact with other cultural groups.

Furthermore, the exact nature of Holocene trade routes and subsequent cultural contacts, are still debated. Although Pleistocene migration and colonisation continues to be explored with increasing archaeological fieldwork by a number of collaborative teams in northern Australia and Island Southeast Asia (ISEA), less research has focused on potential Holocene contact. Sea-faring peoples presumably brought the dingo to Australia, yet little is known about them. Were these seafarers part of a wave of human migrations that contributed to the current Aboriginal gene pool (as controversially proposed by [Pugach et al., 2013](#); see below) or were they early transient merchants who traded the dingo as a commodity for other goods? Did the dingo arrive by accident, the result of mid-Holocene shipwrecks off Australia's northern shores? It has been proposed by Alan Wilton that Australian dingoes could conceivably have descended from a single pregnant dog (in [Dayton, 2003](#)). Resolving the origin of the dingo could potentially alter our current understanding of some of these significant Holocene changes, while at the same time adding valuable information to the opacity encasing the movement of people around Oceania during the Pleistocene and Holocene (c.f. [O'Connell and Allen, 2004](#); [Rasmussen et al., 2011](#)).

2.2. Archaeological evidence for dingoes

To date, the most comprehensive study on the dingo has been based on observable morphological and metrical characteristics ([Gollan, 1980](#)). The origin of the dingo is still an enigma, partly because of the limited efficacy of purely morphological approaches in resolving

Table 1
Summary of recent genetic research with implications for dingo origins.

Study	Method	Samples	Probable origin	Probable route	Arrival in Australia
Savolainen et al. (2004)	mtDNA; identified mtDNA type A29	211 dingoes, 676 dogs, 38 Eurasian wolves, 19 pre-European archaeological Polynesian dog samples	East Asia	South China to Taiwan, the Philippines, ISEA and into Australia	c. 5000–6000 BP
Oskarsson et al. (2011)	mtDNA; mapping of haplotypes A29, Arc1, Arc2	674 dogs, 232 dingoes, 3 NCSD	South China; NCSD and dingoes share a common ancestor SE Asia to New Guinea	South China to MSEA to Indonesia to Australia	4600–18,300 BP
Ardalan et al. (2012)	Y-chromosome (SNPs); haplotypes H3, H60	2 dingoes (47 characterized), 1 NCSD	SE Asia to New Guinea	New Guinea	–
Sacks et al. (2013)	Y-chromosome (SNPs)	338 dingoes, NG singing dogs, SE Asian dogs, modern European breeds	SE Asia and Taiwan	Taiwan	4000–5000 BP
Freedman et al. (2014)	Whole genome sequencing (SNPs)	1 dingo, 1 basenji, 1 golden jackal, 3 wolves	China	–	–
Greig et al. (2015)	Complete mitochondrial genomes (mitogenomes) sequenced	14 colonisation era dogs from Wairu Bar, NZ	China	Southern China to MSEA, Borneo, Sulawesi to northern Australia	–
Shannon et al. (2015)	Mitochondrial and Y chromosome diversity	4676 purebred dogs (161 breeds), 549 village dogs from 38 countries (no dingoes sampled)	Central Asia (Nepal/Mongolia)	–	–

phylogeography, and partly because the process of wolf domestication is still poorly understood (Freedman et al., 2014; Larson and Bradley, 2014). These factors have stood in the way of resolving the genetic origins of both domestic dogs and dingoes. Archaeological and morphological research suggests that the dingo most probably originated somewhere in Asia – India (Gollan, 1985), southern China and various parts of Southeast Asia (Corbett, 2001) have all been proposed (Fig. 1).

Wherever their geographic origin, dingoes were likely brought to Australia by people, either as a product of trade, migration or commensal relationships. Early archaeological evidence suggests that dingoes were widespread within Australia by c. 3500 years ago, with skeletal evidence uncovered in a variety of geographic locations including Western Australia (Madura Cave, Nullarbor 3450 years ago; see Milham and Thompson, 1976), New South Wales (Wombah Midden, 3230 years ago; McBryde, 1982) and Victoria (Fromm's Landing, 3170 years ago; Mulvaney et al., 1964). The dingo features prominently in Aboriginal mythology throughout Australia (e.g. see Rose, 1992), and its importance is further bolstered by the discovery of intentional dingo burials from Arnhem Land (Gunn et al., 2010) and several sites across south-eastern Australia (Gollan, 1980, 1984; Pardoe, 1996). Archaeological (Gunn et al., 2010) and ethnographic (Cahir and Clark, 2013) evidence suggests that the dingo was viewed in a variety of ways – ranging from a hunting companion and camp dog to food source (see also Corbett, 2001).

Artistic representations of dingoes at rock art sites are generally rare across Australia (Pardoe, 1996). However, there are several images from Arnhem Land (Gunn et al., 2010) and other places across the continent. Dingo paw stencils are known from both New South Wales and the Northern Territory (Gunn et al., 2010; Taçon et al., 2010). One of the most impressive sites with dingo imagery is 'Dingo's Lair' in Wollemi National Park, New South Wales with several close to life-size naturalistic depictions drawn with charcoal (see Fig. 2 and Taçon et al., 2012). At a few locations dingoes are depicted in association with humans, such as in Kakadu National Park and the Laura region of north Queensland (Fig. 3).

2.3. Dog domestication

Our understanding of the phylogeographic history of dingoes has arisen out of broader research on dog domestication. Current genetic studies on dogs in general fall into one of two camps: some suggest a single domestication 'event' in one geographic area, with a subsequent extinction of the ancestral wolf population (Freedman et al., 2014), while others propose dogs were domesticated multiple times in multiple places from local wolf populations (Skoglund et al., 2011; Vilà et al., 1997). Some researchers suggest origins at varying times in places as widespread as Southeast Asia/China (Ding et al., 2012; Oskarsson et al., 2011; Pang et al., 2009; Sacks et al., 2013; Savolainen et al., 2002) the Middle East (vonHoldt et al., 2010), central Asia (Druzhkova et al., 2013), Europe (Germonpré et al., 2009; Thalmann et al., 2013), Africa (Boyko et al., 2009) and the Americas (Van Asch et al., 2013), or some combination thereof (Brown et al., 2011; Vilà et al., 1997). As is clearly apparent, genetic studies of modern dog breeds have yet to pin down the exact timing and location of dog domestication. This is in part due to the complex nature of the process (see Larson and Fuller, 2014), potentially involving numerous backcrossings with wolves from multiple populations over time, accompanied by several independent domestication events and genetic bottlenecks (Axelsson et al., 2013; Boudadi-Maligne and Escarguel, 2014; Parker et al., 2010).

Archaeologically, it also remains elusive whether domestic dogs have single (Freedman et al., 2014) or multiple (Larson et al., 2012) origins, as well as the exact geographic location(s) and timing of their domestication. Perhaps because morphological differences between wolves and early domestic dogs may be slight, and early archaeological evidence is fragmentary (obscuring physical differentiation by traditional zooarchaeological methods), it has been difficult to establish whether canids recovered from archaeological contexts represent wild or early domesticated individuals. Archaeological associations between wolf remains and early hominids in China and Europe dated to between 150,000 to 400,000 years ago (Clutton-Brock, 1995; Olsen, 1985) suggest at the very least shared hunting habitats and perhaps predation

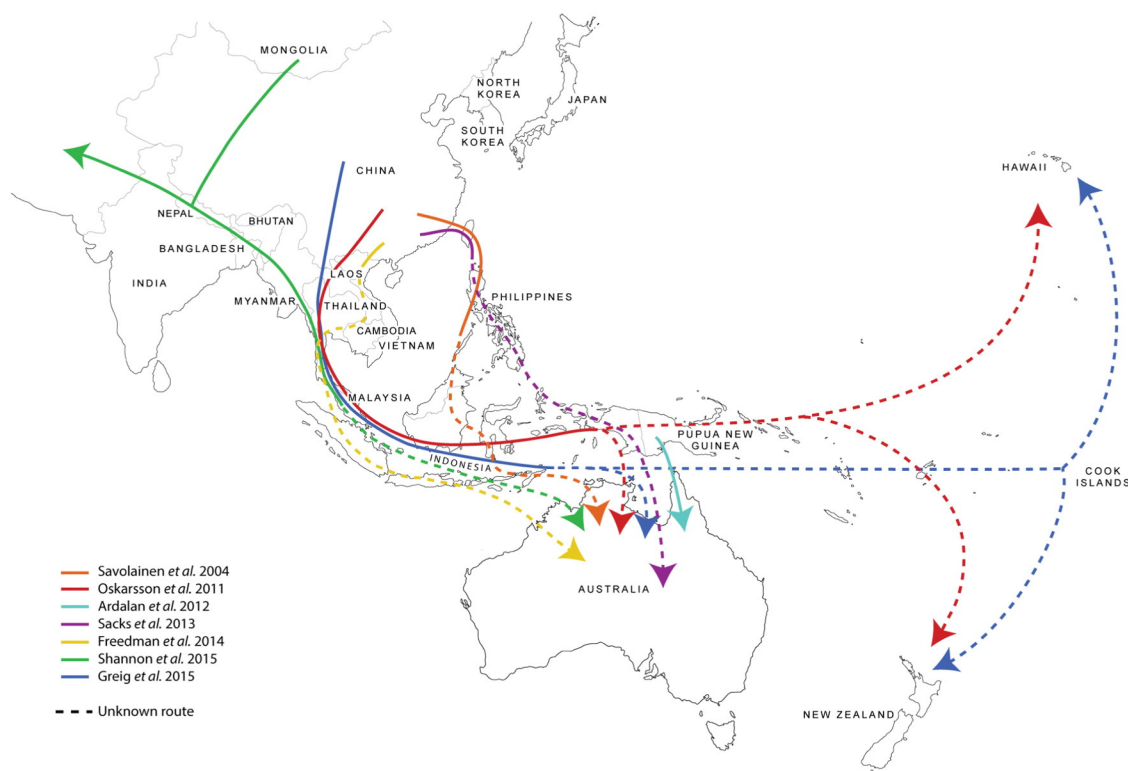


Fig. 1. Map depicting possible phylogeographic origins of dingoes, based on recent genetic evidence.



Fig. 2. Rock drawings of dingoes, Dingo's Lair, Wollemi National Park, New South Wales, Australia.

in both directions. However, archaeological evidence for dog domestication is much more recent, with the earliest potential physical evidence for large dogs from the Altai Mountains of Siberia, c. 33,000 years ago (Ovodov et al., 2011) and Goyet, Belgium, c. 31,700 years ago (Germonpré et al., 2009). The footprints of a large canid argued to be part wolf, part-dog were found alongside those of an eight to ten year old boy in Chauvet Cave, southern France, where soot and smudge marks have been dated to c. 25,000–26,000 years ago (Garcia, 2005). This could be the earliest surviving evidence of a close human/wolf/dog relationship (but see Shipman, 2015). Interestingly, much of this early evidence for domesticated dogs has been recently questioned and debated, resulting in some suggesting a revised domestication date ranging from 11,000–18,000 (Crockford and Kuzmin, 2012; Morey, 2014 but see Germonpré et al., 2015). Perhaps the absence of dogs in Australia prior to the Holocene might lend support to a more recent date for the domestication of dogs world-wide.

Evidence for large dogs dating from about 14,000 years ago across the Ukraine (Pidoplichko, 1998; Sablin and Khlopachev, 2002, 2003) and Russia (Germonpré et al., 2009; Gvozdozer, 1995) is increasingly common while small domestic dogs also occurred in Europe during the Upper Palaeolithic, from at least 15,000–11,500 years ago (Pionnier-Capitan et al., 2011). Dog remains buried together with humans in Israel, dated to 11,000–12,000 years ago, at present constitute the oldest undisputed archaeological evidence of the domestic dog (Davis and Valla, 1978). However, dog burials per se are very widespread within archaeological contexts in both the Old and New Worlds (Morey, 2006), with early Holocene dog burials found from Portugal (c. 8000 years ago; see Detry and Cardoso, 2010) to Siberia (c. 7000 years ago; see Losey et al., 2011).

Closer to Australia, evidence for early dog domestication is sparse. In Northern Vietnam there is evidence for domestic dog dated to 4000 cal. BP associated with the Phung Nguyen Culture, which likely



Fig. 3. Rock painting of a dingo and Ancestral figure, Laura region, Queensland, Australia.



Fig. 4. Rock painting of a dog with men, a woman and child, Thailand.

spread from southern China (Piper, *in press*). According to Piper (*in press*), this radiation of domestic dogs corresponds well with a proposed expansion of Austroasiatic speaking populations from southern China into parts of mainland South East Asia (MSEA). There is also strong skeletal evidence from several sites in Thailand, as well as depiction in rock art (Fig. 4). In ISEA the most secure evidence for dogs dates to c. 3000 BP from a dog burial from Timor-Leste (c.f. Gonzalez et al., 2013). The dog from Timor-Leste is thought to be morphologically similar to village dogs of eastern Indonesia and the Pacific, which have been argued to be distinct from Australian dingoes (Gonzalez et al., 2013). This difference suggests there were at least two initial radiations of dogs into ISEA, one of which came to Australia. This idea is supported by genetic analysis (Sacks et al., 2013) and by broader thinking on dog domestication in general (Larson et al., 2012).

3. Summary of recent genetic research on dingoes

At present, the phylogenetic history of dingoes is opaque. In much of the research on dog domestication, dingoes have not figured prominently; their inclusion is often tangential, with molecular work carried out on modern dingoes that carry the DNA of recent, European dog breeds. Our focus here is on synthesizing the methods used in the various studies to provide a deeper understanding of our current knowledge base. We then discuss the contributions the genetic evidence makes to our present understanding of the dingo's phylogeographic origins by evaluating this data against a likely list of cultural groups who could have brought this new commensal to Australia.

Current research on modern dingoes has used a combination of mitochondrial DNA (mtDNA) (Freedman et al., 2014; Oskarsson et al.,



Fig. 5. Australian dingo, Kakadu National Park, Northern Territory, Australia, 2013.



Fig. 6. North Borneo dog, Niah, Sarawak, Malaysia, 2012.

2011; Savolainen et al., 2004; Wilton et al., 1999), Y-chromosome DNA (Ardalan et al., 2012; Sacks et al., 2013), and nuclear DNA, specifically variation at microsatellite loci (Wilton et al., 1999) (Table 1). These data suggest that dingoes are likely descendants of Asian dogs (and therefore likely Asian wolves). But is their origin in China, Mongolia/Nepal, Thailand, or elsewhere? Did dingoes diverge from local wolf populations in East Asia between 11.8 and 13.7 years ago (Freedman et al., 2014), or were they descended from the Asian (Chinese) wolf (vonHoldt et al., 2010), and were part of a group of ‘ancient’ breeds that may have arrived in Australia around 5000 years ago (Savolainen et al., 2002, 2004), or even as early as c. 18,000 years ago (Oskarsson et al., 2011)? While an 18,000 year date is unlikely given their absence from Tasmania, which became isolated from mainland Australia by rising sea levels c. 12,000 years ago, it is possible their arrival here is a significantly older than the 3500 year date suggested by the limited archaeological evidence (Milham and Thompson, 1976). Molecular studies have variously suggested that the dingo has a close affinity to the New Guinea singing dog (Savolainen et al., 2004) and/or Bali dogs (Sacks et al., 2013), as well as dogs of Borneo (Oskarsson et al., 2011; compare Figs. 5 and 6).

3.1. Mitochondrial DNA

Mitochondrial DNA (mtDNA) is frequently used in research on animal domestication. Mitochondrial DNA exist outside of the cell nucleus, are maternally inherited, and each of the nearly 2000 mitochondria in every cell contain several copies of their own genome (Matisoo-Smith and Horsburgh, 2012). Mitochondrial DNA can provide information on the way in which mutations occur in non-coding base pairs of DNA, specifically by examining changes or substitutions in base pairs, known as single nucleotide polymorphisms (SNPs). These changes can then be used as a tool for examining inheritance in ancient populations in two main ways: first by clarifying the genetic relationships between species; and second by examining the relatedness of last common ancestors to trace ancestry. While a powerful tool with the ability to differentiate between species, mtDNA cannot be used to differentiate between individuals at a finer scale – such as the differentiation needed to distinguish between dog breeds (Larson, 2011). For this reason, gene sequencing

from the nuclear non-coding genome using microsatellites (STRs) has also been used. Microsatellites can be used to analyse populations by differentiating between breeds, and so have been used to distinguish dingoes from dogs (Wilton et al., 1999).

Although mtDNA cannot differentiate dingoes from other ‘breeds’ of dog, haplotypes can be a powerful tool for tracing inheritance and genetic ancestry (and therefore spatio-temporal origin). For instance, mitochondrial variation at the control region is low in dingoes, with over 50% of animals sampled possessing haplotype A29 (a DNA sequence with a specific combination of mutations) (Oskarsson et al., 2011; Savolainen et al., 2004). This haplotype is shared with dogs from East Asia, the Southeast Asian islands and Arctic America (Savolainen et al., 2004). Oskarsson et al. (2011) mapped the distribution of the mtDNA dingo founder haplotype A29 along with the founder haplotypes present in ancient Polynesian dogs (Arc1 and Arc2) in modern samples of dogs across southern East Asia and Island Southeast Asia (ISEA). They found all three haplotypes were present in samples from south China, mainland Southeast Asia and Indonesia, and absent from Taiwanese and Philippine samples. Oskarsson et al.'s (2011) results suggest that dingoes originated from dogs with a probable south China origin that were introduced to Indonesia via mainland Southeast Asia (MSEA) prior to the Taiwanese Neolithic (c. 5500 years ago); mitochondrial diversity in dingoes suggests a much older date of introduction to Australia, ranging from 4600 to 18,300 years ago (Table 1).

In a similar vein, Freedman et al. (2014) used polymorphism data from 10 million SNPs to carry out whole genome sequencing on domestic dogs. Their study sought to examine lineage characteristics for AMY2B expansion (the gene that codes for cereal digestion), as well as to provide estimates of past population sizes based on genome-wide patterns of heterozygosity using advanced statistical methods. Using dingoes as one of their base lineages and heterozygosity rates drawn from a sample of modern dingoes, they estimated a dingo population size at 3000 years ago to have been 704–1042 individuals (assuming a three year generation time). A non-parametric test for gene flow between two divergent populations indicated significant admixture between dingoes and other lineages ancestral to the contemporary sample used (Freedman et al., 2014: 4–5). These findings suggest ancient admixture most likely reflects ancestral breeding with early

Eastern Eurasian-type canines, and is “supported by evidence for bidirectional gene flow between dingoes and wolves using Bayesian statistical analyses, suggesting a divergence from wolves around 11.8–13.7 kya” (Freedman et al., 2014: 5). They further suggest a single origin for dogs (disfavoring the alternative hypothesis that different dog lineages arose from distinct wolf populations), estimating a recent divergence between dogs and wolves between 11 and 16,000 years ago. Freedman et al.’s (2014) inability to find a geographic origin for this event led them to hypothesize that the original population of wolves from which dogs descended is now extinct. Importantly, their data supports a pre-agriculture origin for dogs, suggesting that dogs originated with hunter-gatherer groups. Importantly, dingoes were found to have only two copies of the starch digestion gene (AMY2B), suggesting dingoes were not part of an agricultural package – and so were unlikely brought to Australia by a Neolithic expansion of agricultural peoples into ISEA.

3.2. Y-chromosomes

Y-chromosomes have also recently been used to examine dingo ancestry. Unlike the maternally inherited mtDNA, the Y-chromosome is paternally inherited. Ardalan et al. (2012) built on Oskarsson et al.’s (2011) work by sequencing base pairs from the Y-chromosome of two dingoes and one New Guinea singing dog (NGSD), applying their results to the characterization of a modern sample of male dingoes. Their study found two haplotypes (H3 and H60) common to Southeast Asian dogs, with H60 unique to dingoes and NGSDs. Ardalan et al.’s (2012) findings show very low Y-chromosome diversity, similar to the low diversity shown by the unique occurrence of haplotype 29 using mtDNA by Oskarsson et al. (2011). The implications of their study suggest that the dingo was likely introduced once from a single geographic location (New Guinea), and then spread throughout Australia. They suggest that genetic bottlenecks could explain the low genetic diversity in dingoes, augmented by a small founding population that was subsequently genetically isolated.

Sacks et al. (2013) also examined the Y-chromosome for clues to the dingo’s ancestry, using an expanded sample of 29 SNPs and 5 STRs from a large sample of dogs (338), including dingoes, New Guinea singing dogs, village dogs from Southeast Asia and modern European breeds. Their aim was to resolve the lack of genealogical resolution and mutation rate estimates currently affecting other studies of patrilineal markers. They found that dingoes possessed a unique haplogroup characterized by a single distinguishing SNP mutation and 14 STR haplotypes.

Sacks et al. (2013) estimated a younger age for the origin of the dingo (c. 4000–5000 years ago) – sometime during the Southeast Asian Neolithic, as opposed to the older Palaeolithic dates suggested by both Oskarsson et al. (2011) and Ardalan et al. (2012). They argue that dogs were not originally domesticated in Southeast Asia, instead proposing a Neolithic expansion of dogs from Southeast Asia partially replaced dogs from the West. Their data supports the hypothesis that the dingo and New Guinea singing dog predate the dogs of ISEA, reflecting the last vestiges of this early South East Asian dog. They also support a Taiwanese origin for the dingo.

4. Discussion

Despite different approaches, several common threads run through much of the current genetic research on dingoes. Among these are an Asian origin (China, Taiwan, Island Southeast Asia) (see Table 1, Fig. 1), an arrival date between 5000 and 12,000 years ago, and a genetic affinity between dingoes and New Guinea singing dogs (whether the two breeds are descendent from a common ancestor or otherwise related is still unresolved). Clarifying this phylogeographic and genetic enigma will provide information on the movement of people during the Holocene, including contact between people of Asia and Australia. In

particular, it is commonly thought that Aboriginal populations were in relative genetic isolation from the Pleistocene to European contact, although recent rock art dating suggests contact with Macassan and other Southeast Asian fisherman may have begun much earlier than previously thought (Taçon et al., 2010).

Given the combination of archaeological and genetic evidence, there are several groups of people who could have brought the dingo to Australia. Most of the genetic data is broadly in agreement on a translocation route through ISEA – with many suggesting a path via Indonesia rather than Papua New Guinea. On this basis, we suggest there are five groups of peoples who could have brought the dingo to Australia: 1) Mariners from India, 2) Lapita peoples, 3) a Timor group 4) a Taiwan group, and 5) Toalean hunter-gatherers from south Sulawesi.

4.1. Could Indian mariners have brought the dingo?

Recent controversial genetic research suggests significant gene flow between Aboriginal people and south Indian populations during the mid-Holocene, around 4200 years ago (Pugach et al., 2013). The authors argue this may account for the arrival of the dingo with a time of 4200 years ago in agreement with archaeological studies. Yet while Pugach et al.’s study corroborates data previously suggested by preliminary analyses of mtDNA sequences (Gunnarsdóttir et al., 2011), and Y chromosomal studies (Redd et al., 2002), it has caused heated debate (see Brown, 2013; Price and Bird, 2013; Pugach and Stoneking, 2013) – specifically with respect to the timing of contact and Holocene changes within Australia.

Pugach et al. (2013: 5) suggest a contact time of 4230 years ago based on admixture 141 generations ago, assuming ‘a generation time of 30 y’. However, this calculation may not be precise as Krzywicki (1934) has shown that among Australian hunter-gatherers a generation time could be as low as 15 years (it is rare to give birth after 30, and 30 year old women are grandmothers), while Fenner (2005) has argued a mean of 25.6 should be used for female hunter-gathers (taking into account of mother’s age for both first and last births). He also argues that if both males and females are included, the best generational interval for hunter-gatherers is 28.6. Therefore, if Pugach et al.’s other assumptions are correct and there was a visit from India, it could have occurred any time between 2115 to about 4033 years ago, most of which is well after the dingo is known to have been in Australia. Problems with their dating are further highlighted by their estimated divergence time between Aboriginal Australians, New Guineans and a Philippines Negrito group at about 36,000 years ago, rather than at least 45,000 years ago as indicated from archaeological evidence of human presence in Australia (Brown, 2013). If the same percentage of error occurred with their estimation of contact between Aboriginal Australians and a group from India then it would have occurred 5250 years ago. This highlights a lack of fit between the genetic and archaeological clock that needs to be addressed in future studies.

Pugach et al.’s (2013) study also failed to consider the implication of the results of DNA research on dingoes (Brown, 2013; Price and Bird, 2013) – despite analysing and comparing human DNA. Existing genetic studies do not support an Indian origin for the dingo. Pugach et al. instead emphasized morphological similarities between dingoes and some Indian dogs (Pugach et al., 2013: 5), an approach used several decades ago (e.g. Gollan, 1985). However, molecular results from dingoes could be used to evaluate Pugach et al.’s (2013) hypothesis and those of others, as dingo DNA can be interrogated for a variety of geographic origins, and then compared to similar human molecular data. Such an approach would facilitate unprecedented clarification of potential recent Holocene human movement, and migration routes, which could then be correlated with the archaeological record. This would enable us to test whether dingoes were brought to Australia by hunter-gatherers or by early agriculturalists.

4.2. Could Lapita peoples have brought the dingo?

The origin of Lapita culture has been the subject of ongoing debate but generally it is agreed to have originated after 3500 years ago and primarily spread eastward across the Pacific islands (e.g. see Spriggs, 1999, 2000). Recently, the origin date has been placed closer to 3000 years (e.g. Sheppard et al., 2015). As archaeological evidence shows the dingo was widespread in Australia by this time, it is improbable that Lapita peoples brought the dingo. Furthermore, there is no evidence to suggest that the pig or the chicken was introduced into Australia when the first dogs arrived, as has been argued to occur wherever Lapita peoples ventured. At present, there is no confirmed evidence of Lapita pottery from mainland Australia, something that characterized the movement of Lapita peoples throughout the Pacific. The later Neolithic arrival of Lapita peoples to the Pacific, coupled with the absence of dog in early Lapita sites (Piper, in press), suggests dogs may have been introduced to ISEA earlier, and were therefore not a part of the Austronesian cultural package, as has been proposed by various scholars (e.g. Bellwood, among others). The archaeological evidence also fits well with molecular evidence for the A29 haplotype (Oskarsson et al., 2011, Table 1, Fig. 1), suggesting a route via MSEA and Indonesia (not Eastern South East Asia/Pacific).

4.3. Could Timor peoples have brought the dingo?

Timor is close to northern Australia but the earliest evidence of dog dates to a burial that has been securely dated to 3000 BP (Gonzalez et al., 2013). Since dingoes were widespread in Australia by c. 3500 years ago, this is too recent (see above). Furthermore, this Timor-Leste dog is morphologically distinct from Australian dingoes, and is most similar to village dogs of eastern Indonesia and the Pacific. Isotopic analysis from the remains produced 'Isotope values which indicate a diet dominated by terrestrial plant foods rather than hunted foods suggest an association between the Timor dog and agriculturalists' (Gonzalez et al., 2013: 13) and a diet similar to Pacific pigs (Gonzalez et al., 2013: 14). This hints at a Neolithic origin for the Timor dog, and is supported by DNA studies that indicated that the partial sequence obtained was identical to Asian and Asian-derived breeds (Gonzalez et al., 2013: 14–15; Savolainen et al., 2004). However, a relationship to dingo DNA has not yet been undertaken.

Additional archaeological evidence suggests a later arrival of dogs to Timor, such as the late arrival of pottery c. 3500 years ago (O'Connor, 2015: 24). O'Connor (2015: 27) concludes the dog did not arrive in Timor until after 3200 years ago, and that a marsupial, *Phalanger orientalis* (northern common cuscus), was introduced to Timor-Leste about the same time. In this case, archaeological and genetic evidence are all in agreement – suggesting the dingo came from somewhere else.

4.4. Could Taiwanese people have brought the dingo?

Did dingoes arrive as part of a fast (Bellwood, 1997; Diamond, 1988, 2001) or slow (O'Connor, 2004; Solheim, 1996) Austronesian expansion out of Taiwan as Sacks et al.'s (2013) results support? This seems highly unlikely given recent reviews of archaeological and other evidence across ISEA to Australia's immediate north that show complex interaction in various directions between many groups in this region, not only in the past 4000 years but also extending back into the Pleistocene (e.g. Bulbeck, 2008; O'Connor, 2015). Indeed, the nature of Austronesian expansion was not neat in this region at all, with many indigenous cultural developments combined with contact and trade with a range of people from Taiwan to Vietnam to peninsular Malaysia. Genetic (and morphological) evidence also suggests dingoes are unrelated to modern village dogs of eastern Indonesia and the Pacific (Sacks et al., 2013). Further, dingoes lack the gene to digest cereals suggesting they did not accompany agricultural peoples from this area (Freedman et al., 2014). According to Piper (in press: 268), "it's likely two lineages of

dogs were introduced to ISEA, the dingo and the village dog." This village dog, also discussed by Shannon et al. (2015), may explain why evidence for Taiwanese dogs exists that does not fit with the genetic evidence for dingoes. It seems very plausible that a later radiation of dogs spread through eastern Indonesia and the Pacific, from Taiwan, but this is a suggestion that needs significantly more data.

4.5. Could Toalean or other south Sulawesi peoples have brought the dingo?

Bulbeck (2008) presents evidence for a cross-sea interaction sphere from between 4000 and 2500 BP across ISEA, including between Borneo and Sulawesi. He also argues for long-term maritime interaction prior to this period, especially among hunter-gatherers between south Sulawesi and Borneo. Archaeological evidence indicates maritime hunter-gatherers engaged in deep sea fishing off nearby Timor 42,000 years ago. For instance, at Jerimalai cave 'Bones from pelagic fish, such as tuna, compose almost 50% of the total fish assemblage in the earliest occupation layers' (O'Connor et al., 2011: 1118) but also 24–46% of other layers (see also Anderson, 2013; O'Connor and Ono, 2013 reply). And fishhooks are found in terminal Pleistocene layers – all evidence supporting long-term contact between peoples of this region. Furthermore, a sophisticated maritime hunter-gatherer culture is suggested to have been widespread across the area for over 40,000 years, resulting in the initial colonisation of Australia, among other things (O'Connell and Allen, 2012). All of this supports the possibility of maritime hunter-gatherers bringing the dingo from Borneo to Australia, as Oskarsson et al.'s (2011) study suggests, possibly via people in south Sulawesi.

Unfortunately, dog has not yet been found in south Sulawesi archaeological sites. In west Sulawesi dog is found 'in the earliest Neolithic levels of the Karama valley sites' (O'Connor, 2015: 41), dated to about 1000 BP (Anngraeni et al., 2014; O'Connor, 2015: 25). Since at least the 1600s Makassan and other people from south Sulawesi have been visiting northern Australia and participating in exchange networks with Aboriginal Australians (Taçon et al., 2010), reaching a peak of annual visitation in the late 1700s through the 1800s (Macknight, 1976, 1986, 2008). The ease with which Makassans reached northern Australia underscores the possibility of much earlier visits. And prior to the presumed dingo arrival date in Australia, a culture named the Toalean occupied south Sulawesi (Bulbeck, 2000) – the term 'Toalean' specifically 'applied to microlithic assemblages in south Sulawesi with an age range between c. 8000 and 1500 BP' (Bulbeck, 2000: 71). These were hunter-gatherers able to travel vast distances by sea (Bulbeck, 2000: 94) who eventually encountered and absorbed Austronesian farmers rather than being replaced by them (Bulbeck, 2000: 101–103).

Of all groups discussed above, the Toalean appear to be the strongest candidates for bringing the dingo to Australia, perhaps after obtaining it from people in Borneo. The lack of the starch digestion gene (AMY2B) in dingoes lends further support to their accompanying a hunting and gathering people, as opposed to peoples from an agricultural society, but this hypothesis needs to be tested in other ways, including a genetic study of dog remains from archaeological contexts. Additionally, this idea must be examined against the context of variability in subsistence strategies around Oceania during this time, as MSEA was likely a village environment with agriculturalists while in ISEA there was no agriculture. It's possible that dogs were moving back and forth between agriculture/no agriculture, and thus there were different human-dog relationships at the same time, which we are interpreting as Piper's (in press) two lineages. However, one of the challenges facing this route is the lack of dog remains from most ISEA archaeological sites (Larson et al., 2012; Piper, in press), including those of south Sulawesi. And in this regard we need to be careful we do not interpret this lack of evidence as evidence of absence – many early dogs remains simply may not have survived across Island Southeast Asia, or we have not excavated places likely to contain them. Sulawesi should therefore be viewed as a starting point.

4.6. The way forward

We suggest that to resolve the dingo's origin, and thereby clarify human cultural interactions and transformations in Holocene Australia, the following inter-related steps could be taken:

We need a focus on aDNA as opposed to other genetic methods. Previous work has relied largely on mtDNA which has proved limiting for the fine-scale resolution data needed to differentiate between dog breeds and thus questions surrounding geographic/temporal origin (Larson and Bradley, 2014; Larson, 2011; Parker et al., 2004). An approach that uses information from across the nuclear genome (as opposed to mtDNA) may have greater potential benefit, as it contains the genes that code for the differences between wild and domestic individuals. Additionally, the nuclear genome has the potential to distinguish between pure dingoes and dingo-hybrids, and to estimate past population sizes, time since genetic divergence and the degree of species introgression.

Pre-contact dingoes must be sampled. The recent (post-European contact) hybridization of dingoes with modern dog breeds is estimated to affect 80% of the modern population of dingoes (Crowther et al., 2014). This is further complicated by using modern data to infer ancient phylogeographic/phylogenetic patterns rather than using ancient DNA to actually define what these patterns are.

Archaeological samples must be used to compare ancient potential canine ancestors (i.e. archaeological/fossil New Guinea singing dogs, Pukapuka dogs, Indian dogs, MSEA and ISEA dogs, and southern Chinese dogs), with phylogenetic analyses performed to estimate their relationships. For instance, dog mandibles have been recovered from the West Mouth of Niah Cave and Lubang Kudih in Sarawak (Clutton-Brock, 1959; Medway, 1959, 1977) and these examples would be useful for testing the Borneo origin of dingoes promoted by Oskarsson et al. (2011), along with the Karama Valley dog remains of West Sulawesi discussed above.

Collaboration between archaeologists and geneticists (evident in all of the dingo research to date) must be stronger, as repeatedly suggested (cf. Germonpré et al., 2015; Larson et al., 2012; Morey, 2014). Both records provide unique information but both have different sorts of problems. If both good archaeology and good genetics are practiced in an integrated fashion within a project, then robust results with high explanatory power should be obtained. But at the same time we also need to be careful to avoid circular arguments and be open to the unexpected, rather than massaging results from one discipline to fit perceived results from the other (see Larson et al., 2012 for a good critical discussion).

Archaeological and genetic evidence must be integrated with comparative phylogeography, whereby genetic markers can be used to track the colonisation and demographic history of dingoes by fitting their genealogies to geographical and temporal frameworks (c.f. Jones et al., 2013). As recent research has acknowledged, 'Given the fact that domestic animals were always a key part of the migratory package, the genetic signals derived from their remains can act as a proxy for human migration' (Larson, 2011: S493).

5. Conclusion

Dogs accompanied people into all corners of the globe, and this relationship can be used as a proxy for understanding the movement of people and ideas around Oceania during the Holocene. While the dingo's exact translocation route to Australia is currently unknown, clarity is within reach. As demonstrated here, recent genetic research on dingoes can be used to evaluate a potential list of peoples who could have brought the dingo to Australia. This list, and ensuing discussion, suggests that Sulawesi may be a starting point. Australia represents the terminal points for migration of commensal canines so unpacking the dingo's phylogenetic and phylogeographic history will provide key information behind big theoretical questions – such as where, how

and why people are moving. The answers to these questions excellent potential to better understand human contact in this still enigmatic part of the world.

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